Odonatologica 7 (3): 263-276 *September 1, 1978*

A COMPUTER MODEL OF THE GROWTH OF LARVAL DRAGONFLIES

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Received August 3, 1977 / Accepted January 16, 1978

A computer model was constructed using the bioenergetics data of J.H. LAWTON (*Hydrobiologia* 36 1970: 33-52; *J. anim. Ecol.* 39 1970: 669-684, 40 1971: 395-423; *Freshwat. Biol.* 1 1971: 99-111) on *Pyrrhosoma nymphula.* Model predictions of the growth of an individual dragonfly were compared to Lawton's data on length to test the model. Comparisons were also made between model predictions and field, literature, and laboratory data for Deep Creek, Oneida County, Idaho, USA, dragonflies, specifically *Argia vivida*, to test the generality of the model. Initially the model equations could not reproduce Lawton's data, but when production and consumption were reduced in the winter months (temperature $< 7°$C), the results were within a mean 10% error of Lawton's original data. Predictions for growth over the complete life cycle were also made with a starting date and initial length as inputs. Laboratory experiments with *A. vivida*, done as part of this study, provided data for tests of the model's ability to make precise short-term predictions. In all but one case presented here, the predictions were statistically different from the observed even when equations specifically for *A. vivida* were used. However, the model as used for Lawton's data did compare well with the field data for the whole life cycle of *A. vivida.* Finally, comparisons were made between *P. nymphula, A. vivida, Enallagma anna, Ophiogomphus severus* and *Diplacodes trivialis* which showed that differences in energy budgets can be related to differences in life histories.

INTRODUCTION

Much of the work on dragonflies has been of a descriptive nature and has concentrated on taxonomy and life histories. Recent research, however, has become more quantitative and experimental in the study of both larvae and adults. One of these recent quantitative studies on the larvae of *Pyrrhosoma nymphula* (Sulz.) (Zygoptera: Coenagrionidae) (LAWTON, 1970a, 1970b;

1971a, 1971b) was the basis for the research presented here. The major objective of this study was to build a predicative computer model which mimics growth of larval dragonflies using data published by Lawton.

Once the model was constructed, the next objective was to test it. Several questions were posed as a guide in testing. First, could the model reproduce Lawton's data? Second, was the model general enough that the growth of other dragonflies could be predicted by the model using Lawton's values and equations for bioenergetic parameters, or were values and equations for the particular species being tested required? Also, was information on all parameters necessary for the model to work, and were there parameters for which better estimates were needed? A third objective was to compare *P. nymphula* with the three main species of dragonflies, *Argia vivida* (Hag.), *Enallagma anna* (Williamson) (Zygoptera: Coenagrionidae) and *Ophiogomphus severus* (Hag.) (Anisoptera: Gomphidae), found in Deep Creek, Oneida County, Idaho in terms of life cycle and habitat, and the values of bioenergetic parameters, since predictions about them would be used to test the model.

A model is a set of relationships (CASTRUCCIO, 1975) between independent variables and a dependent variable or response. In the present study the relationships of the individual parameters to growth needed to be defined. The energy budget, a mathematical expression of the inputs and outputs of energy for an animal (McCULLOUGH, 1975), was the definition used in this model. It can be expressed as the equations:

$$C = P + R + F + U + Ev \qquad (1)$$

and

$$A = P + R \qquad (2)$$

where C is consumption, P is production or growth, R is respiration, A is assimilation, F. is feces, U is excretion (which is usually considered insignificant or unmeasurable), and Ev is exuvia in the case of insects (LAWTON, 1971a). Figure 1 shows diagrammatically how the energy budget was implemented in the model. Since energy budgets have been constructed for the dragonflies of interest, comparisons with the model can easily be made. For *P. nymphula*, Lawton computed the values of the different bioenergetics parameters (except excretion) for both an individual larva and the entire population in a pond. PANDIAN & MATHAVAN (1977) determined the larval energy budget for *Diplacodes trivialis* (Ramb.) (Anisoptera: Libellulidae) in a laboratory study of energy utilization. Partial energy budgets for *A. vivida, E. anna*, and *O. severus* are presented in MINSHALL et al. (1975). Other data for the Deep Creek dragonflies used in the model were taken from BRASS (1971), MINSHALL et al. (1973), and KOSLUCHER & MINSHALL (1973).

METHODS

An IBM model 370/125 computer was used in building and testing the model, and to analyze, tabulate, and graph data. Programs were written in WATFIV and FORTRAN IV (CRESS, DIRKSEN & GRAHAM, 1970). Regression analysis by least squares estimation was used to derive many of the equations in the model. It was also used in comparing the model with laboratory results. Assumptions, equations for calculation, discussion of transformations, interpretation of results, and testing for differences between regression lines for this type of regression analysis are presented in DANIEL & WOOD (1970) and ZAR (1974).

Test data for the model for the Deep Creek dragonflies were collected from short-term (3-4 month) laboratory growth experiments on *Argia vivida* and *Enallagma anna* larvae. Seven bowls with three to five larvae of one species each and 17 beakers with one larva each were used. The experimental design is described elsewhere (NIMZ, 1977).

RESULTS

BUILDING THE MODEL

In building the model, data from LAWTON (1971a) were summarized as means of the bioenergetic parameters for the three year classes studied (NIMZ, 1977). Once the data had been summarized, regression equations were computed

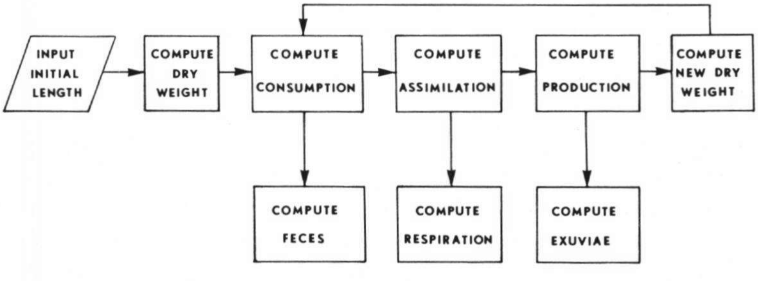

Fig. 1. Flowchart of the calculation of the bioenergetic parameters (after TURNER, 1970). The computations detailed here take place in the main program of the model. The initial length is input on a card, while the other parameters (except exuvia which are a group of constants) are computed within the model. Examples of the forms of equations used in the model are: (2) Dry weight = $10^{(k_1 \log_{10} \text{length} + k_2)}$; – (3) Consumption = $10^{(k_3 \log_{10} \text{temperature} - k_4 - k_5 \log_{10} \text{dry weight})}$; – (4) Feces = Consumption – Assimilation; – (5) Assimilation = k_6 Consumption – k_7; – (6) Respiration = Assimilation – production; – (7) Production = k_8 Assimilation – k_9; – (9) New Dry Weight = Old Dry Weight + Production. – Numbers, e.g. (2), refer to flowchart, k's are constants which are defined in the results)

to relate the paremeters as shown in Figure 1. The r^2 value, which is a measure of explained variation for each equation (ZAR, 1974), plus the degree of simplicity of the regression equation were used to determine which equations were tested for use in the model. For example, simple regression equations were tested instead of equations involving log transformation of the data both because they were simpler and in all cases the r^2 value was higher. For consumption the more complex equations were tested because the simple data and log transformed data regressions of dry weight to consumption had very low r^2 values. This selection process was carried out to minimize the number of equations to be tested. Hence some equations not tested could possibly have been better predictors than those used. To further increase the simplicity of the model, difference equations (RICKER, 1968) were tested for some relationships. These reduced the number of relationships to be defined by regression equations and the amount of data to be collected before other investigators could use the model.

From the group of equations initially selected the best equations for the model were determined by comparing the values generated by each equation within the format of the model with the corresponding original values. This type of testing showed which equations would best reproduce the original data and would be used in the actual testing of the model. For each month, the dry weight and temperature reported by Lawton were the initial values used by equations in the model to predict the values of the bioenergetic parameters. The value from Lawton for a specific month and bioenergetic parameter minus the corresponding model prediction was divided by Lawton's value and defined as the "percent error from Lawton". A mean of the monthly percent errors for each parameter was computed and used as the basis for comparing the different equations. This comparison was used to select the best set of equations for the model. From early tests it was evident that something was lacking in the model. These sets of equations predicted that *Pyrrhosoma nymphula* would emerge one year after oviposition instead of two. Therefore, an examination of monthly comparisons of Lawton and the model was made to see when the error was occurring. In the winter months (Nov.-Mar.) production by the model was much greater than actual production, particularly in the first winter when Lawton measured no production. Also decrease in actual production was shown in another study of *P. nymphula* by MACAN (1974). CORBET (1957) suggested that growth for *Anax junius* stopped at temperatures below 6°C. *P. nymphula* showed reduced growth below 7°C. Both 6°C and 7°C were tested in the model. To allow the model to adjust for the decrease in growth, constraints were imposed on production and consumption. First, consumption was decreased if the temperature was less than 6°C. Then production was set to 0.0 under the same condition. These tests all reduced the error for production, but the differences were still very large, greater than 100%. However, consumption and assimilation were within 5%. Further examination of the data showed that the model predicted assimilation efficiency as a constant 94% (a function of the model design, i.e. assimilation is linearly related to consumption) while for Lawton's data it was 86% to 95%, with one low value of 76% (April of the second year). This indicated that assimilation efficiency did not account for decreased production in the winter. However, the ratio of production to consumption (P/C) did reflect the changes in production. Due to this information, production was multiplied by a constant during both winters. This constant was subjectively determined by the difference between the P/C ratio in the non-winter months and that ratio in the winter months. Two constants were tested for the first winter: 0.12 and 0.001, and one constant for the second: 0.5. Also, consumption was reduced (0.0408 cal/mg dr wt/day) during the winter for these tests when the temperature was less than 7°C. This brought the mean error for all parameters except feces to less than 10%. The increased error in feces was compensated for by the greatly decreased error in production. Based on all of the comparisons, the following equations with reduced consumption and production (multiplied by 0.001 the first winter and 0.5 the second winter) were used for the model predictions of Lawton's data:

$$\log_{10} C = -3.336 + 1.193 \log_{10} T - 0.104 \log_{10} DW \tag{3}$$

$$A = 0.94001\, C - 0.0000688 \tag{4}$$

$$P = 0.62312\, A - 0.000606 \tag{5}$$

$$F = C - A \tag{6}$$

$$R = A - P \tag{7}$$

where C, A, P, F, R are in cal/mg dry wt/day, T is temperature in °C and DW is dry weight in mg. Regression equations 3, 4, and 5 were computed with 23 sets of data, using previously written computer programs (DIXON, 1975). For equation 3 both constants are significantly different from zero and the 95% confidence limits are 1.193 ± 0.589 and

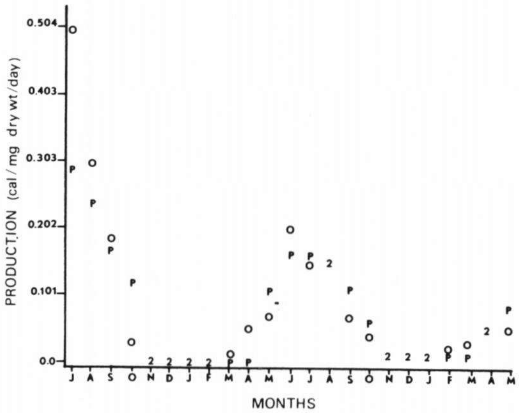

Fig. 2. Comparison of the model with Lawton's data – Production. Lawton's data for production is indicated by an '0'. Production for the model, 'P', was computed with Equation 5 and multiplied by 0.001 the first winter and 0.5 the second winter. Where the two data points for a month coincide this is indicated by a '2'.

-0.124 ± 0.154. The 95% confidence limits for the constants in equations 4 and 5 are 0.94001 ± 0.02401 and 0.62312 ± 0.1340. Comparison between this model and Lawton's data is illustrated in Figure 2 as a graph of predicted and observed production over time.

Each bioenergetic parameter in the model was computed on a daily cycle. An initial length input into the model was used to start the calculations on the first day. The equations which define the mathematical relationships between the parameters were then employed to compute the values of the respective parameters. The resulting production value was added to the initial dry weight to give the starting weight for the next day. This cycle continues until the dragonfly was large enough to emerge. For *Pyrrhosoma nymphula* and *Argia vivida* emergence was defined to occur when length exceeded 15 mm. Equations remained the same throughout the growth of the dragonfly. Any exuviae were arbitrarily produced on the last day of the month a molt occurred. Daily temperatures were the only additional inputs into the model, and they were used along with dry weight to compute the amount of consumption.

TESTS OF THE MODEL

Lawton's data – After equations were selected and conditions for reducing production determined, predictions were made about the life cycle of *Pyrrhosoma nymphula*. The observed lengths (LAWTON, 1971a) are graphed along with the model predictions in Figure 3 and are independent of the bioenergetics data used to construct the model. The initial prediction, which started with a 1 mm dragonfly larva on 1 July, had the adult emerging only 14

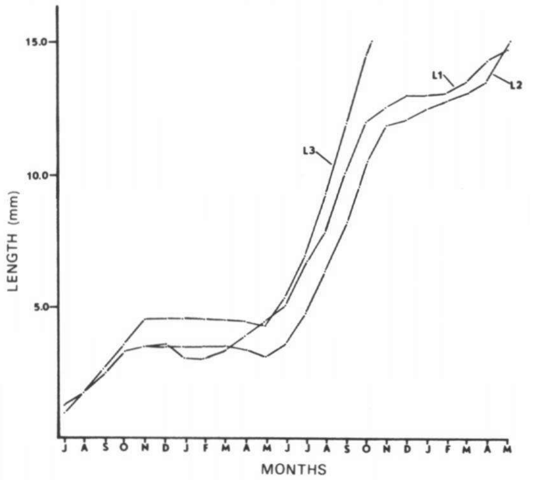

Fig. 3. Model predictions for *Pyrrhosoma nymphula*. This graph compares LAWTON's (1971a) length data (L1) with the predictions of the model. L2 begins with a dragonfly of 3.5 mm on 1 Nov. and predicts emergence on 4 May. (Time of emergence is defined as reaching 15 mm). L3 represents the model's prediction for a starting date of 1 July and initial length of 1 mm. All predictions were made with Equations 3-7, with constraints that if temperature is less than 7°C then consumption is 0.0408 cal/mg dry wt/day and production is multiplied by a constant during the winter months. The constant was 0.001 for the first winter and 0.5 for the second winter.

months later. Since the testing of the equations to be used in the model had shown that the largest difference between the equation generated values and the original data existed in the small size classes, the starting date was advanced one month at a time. The initial length for each month was the length observed by LAWTON (1971a). When a 3.5 mm larva was started on 1 November, emergence was predicted in May of the second year and followed closely the observed larval growth. The predictions for starting dates of 1 August, 1 September and 1 October and the corresponding initial lengths, 1.8 mm, 2.5 mm and 3.3 mm, were emergence dates in October of the second year. The pattern of growth was similar to that for the 1 July starting date in Figure 3.

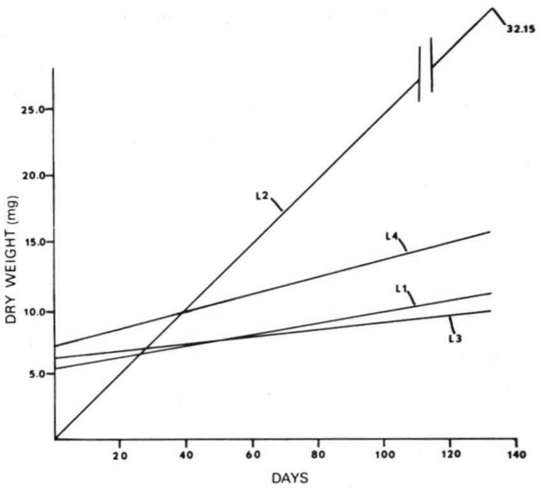

Fig. 4. Comparison of model predictions and the results of the laboratory experiments – bowl # 4. Three sets of equations were used to predict the growth of the laboratory dragonflies. Regression equations were computed for predictions and laboratory data, Dry weight (mg) = 0.0437 Time (days) + 5.23; – the beginning of the experiment. L1 = Laboratory data, Dry weight (mg) = 0.0437 Time (days + 5.23; – L2 = Equations 3-7, Dry weight (mg) = 0.246 Time (days) + 0.0746; – L3 = Equations 4-6, 8, 9, Dry weight (mg) = 0.0263 Time (days) + 6.11; – L4 = Equations 4-6, 8, 10, Dry weight (mg) = 0.066 Time (days + 6.79. – All equations were significantly different in slope according to a Newman-Keuls multiple range test.

Laboratory data – The next phase was to relate predictions of the model to the growth of Deep Creek *Argia vivida* in the laboratory. The data from bowl 4 in the laboratory experiments are used to illustrate the results of these tests. Line L2 in Figure 4 is the model predictions for the growth of the dragonflies in bowl 4. Since these predictions were different statistically and visually, equations from Deep Creek data for consumption and respiration were inserted into the model. A consumption equation was derived from laboratory consumption rates using *Hyallela* as food:

$$\log_{10} C = 0.645 - 0.025\, T - 1.864 \log_{10} DW \qquad (8)$$

Respiration equations for *A. vivida* in flowing water were taken from BRASS (1971):

$$R = 3.29\,DW^{0.58}/DW/0.005;\ \text{at } 18°C \tag{9}$$

$$R = 1.69\,DW^{0.52}/DW/0.005;\ \text{at } 8°C \tag{10}$$

Predictions from sets of equations with both those from Lawton and Deep Creek data are labelled L3 and L4. The regression lines were significantly different from the laboratory data with the exception of L4 (Fig. 4). Equations for all regression lines are listed with the figures.

Deep Creek field data – The final test of the model in this study was a comparison with Deep Creek field data. From data on *Argia vivida* a mean length of a larval dragonfly was computed for each month samples had been taken. In Figure 5 these lengths are plotted (L1) along with two model predictions. These predictions were made with equations from Lawton's data. However, the temperatures were from two different sampling areas at Deep Creek, Stations 1 and 2. Station 1 (L2) is an area of normal fluctuating temperature, while Station 2 (L3) is a constant temperature (18°C) area. Equations from Deep Creek data (Equations 8, 10) were tested. However, the data used to obtain the equations were from the laboratory and were from larvae in the final three instars. The results of model predictions using these equations for the entire life of *A. vivida* were not realistic. For example, a dragonfly of 1 mm was predicted to be 20 mm long at the end of one day.

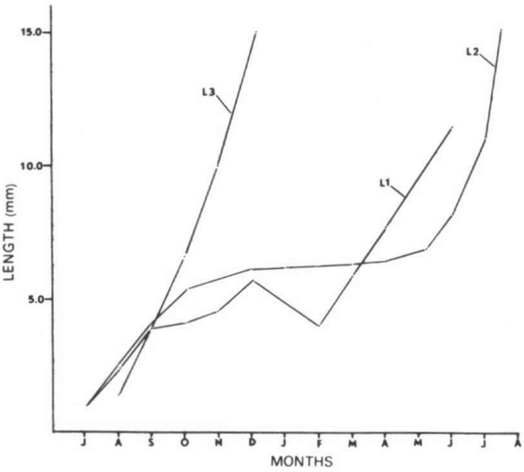

Fig. 5. Comparison of Deep Creek field data with model predictions. L1 is a plot of mean length for each month. These data were from samples taken during 1970-72 for the Deep Creek International Biological Program Study. L2 is the model prediction using Equations 2, 4, 6, 7, 8 from Figure 4 and temperatures from Station 1 at Deep Creek, an area of normal fluctuating temperatures. The temperatures of Station 2 Deep Creek, a constant temperature area, were used with the same equations and resulted in L3.

COMPARISON OF DRAGONFLY ENERGY BUDGETS

Table I allows comparison of the energy budgets of the dragonflies in Deep Creek with those of other species. Only consumption can be compared between the laboratory data for *Argia vivida* in this study and other Deep Creek data. In MINSHALL, ANDREWS, ROSE, SHAW & NEWELL (1975) a value for consumption of 0.778 cal/mg dry wt/day was determined, which is twice the maximum value in this study where the range was 0.0404 to 0.3812 cal/mg dry wt/day. For *Enallagma anna* in the same study production was computed to be 0.041 cal/mg dry wt/day, while in this study it was 0.219 cal/mg dry wt/day for a period of only 24 days.

Table I

Comparison of dragonfly energy budgets. (The energy budgets listed are in cal/larva for the entire larval period (19 months) except for the model budget for *Pyrrhosoma nymphula* which is for 1 Nov. to 4 May. The observed budget for *P. nymphula* is from LAWTON, 1971a: Tab. 10. Data for *Ophiogomphus severus* and *Enallagma anna* are from MINSHALL, ANDREWS, ROSE, SHAW & NEWELL, 1975. For *E. anna* the entire budget is calculated and is not from experiments. The budget for *Argia vivida* is a model prediction from Lawton's equations (Eq. 3-7), using the fluctuating temperatures at Station 1, Deep Creek. The energy budget for *Diplacodes trivialis* is taken from PANDIAN & MATHAVAN, 1977).

	P. nymphula		*A. vivida*	*E. anna*	*O. severus*	*D. trivialis*
	Observed	Model	Model	Calculation	Laboratory	Laboratory
Life Cycle (months)	23	19	12	12	12	4.5
Consumption	189.2	128.5	59.2	92.0	64.5	61.5
Assimilation	166.1	120.5	55.6	80.9	47.5	56.3
Respiration	81.4	56.9	21.6	66.1	19.5	29.2
Feces	23.1	7.5	3.6	11.0	17.0	5.2
Exuvia	4.5	4.4	–	–	–	–
Production	80.2	53.7	34.4	14.9	28.1	27.1
Assimilation Efficiency (%)	88	94	94	88	75	91

DISCUSSION

In testing the model equations against Lawton's data the major problem was the inability to predict winter consumption and production which agreed with the observed values. Two explanations for these differences are proposed. Either the use of the mean temperature for a month as the temperature of each day of that month does not adequately represent the actual temperature fluctuations, or some other factor, such as photoperiod, keys the observed growth reduction in the winter months. If the first explanation is correct, then daily temperatures would be a requirement of this model. The second proposed explanation is part of the ongoing discussion of seasonal regulation, the control of growth by an external factor (CORBET, 1954; LUTZ, 1974a, 1974b). Temperature, photoperiod, or both have been suggested as possibilities. With the incorporation of photoperiod, this model could be valuable in resolving the questions on what controls emergence and diapause in dragonflies.

Model predictions for the entire life cycle of *Pyrrhosoma nymphula* did not agree with the length data from Lawton until the initial length exceeded 3.5 mm. When shorter lengths were tried, the model predicted emergence in 14 months instead of 23 months as observed. The equations used in the model were apparently not adequate for the smaller size classes, and a second set of equations may be needed to make predictions for dragonflies less than 3.5 mm.

When field data for *Argia vivida* and model predictions (with equations from Lawton's data, but without constraints) are plotted on the same graph (Fig. 5), they follow each other closely when normal fluctuating temperatures from Deep Creek are used. However, there are still differences, and again the question of seasonal regulation surfaces, and the need for some key factor other than, or in addition to, temperature in the model is evident. The two sets of temperatures were from two areas of Deep Creek in which emergence begins in May and early June, while the model predicts emergence for the constant temperature area in December.

In the laboratory, short-term (3-4 months) growth experiments with *Argia vivida* and *Enallagma anna* generated additional test data for the model. However, only the data for *A. vivida* were used, and these were reduced because of the similarity of the growth of the larvae in different bowls. The experiments with *E. anna* were limited by the small number of larvae collected and the results were not sufficient to test the model. Although the model equations worked well in predicting growth over an entire life cycle, for short-term experiments (Fig. 4) their predictions were not as close as those made with a combination of equations from Lawton's data and Deep Creek laboratory data. According to a Newman-Keuls multiple range test, all of the predicted lines in Figure 4 were significantly different from the observed line.

Since the predictions for an entire life cycle were compared only subjectively, precise testing of the model at that time was not possible. Therefore, the laboratory data are important in looking closely at the model predictions. Each parameter was computed 30 times for a month and over 300 times in a year during a run of the computer program of the model. This means a small error in the beginning is amplified as the computations proceed, and the predictions get farther and farther away from the observed values. This is illustrated in Figure 4. Each prediction was made with the same initial length as in the laboratory but the end result varied widely. The conclusion drawn is that precise predictions over a short period of time are not possible with this model. It can, however, be used to make general predictions about an entire life cycle of a dragonfly and this was the major objective of the study.

In answer to the last two questions posed in the introduction, information on all parameters is not necessary for the working of the model, and there are parameters for which more precise estimates are necessary. Since all parameters are not explicitly predicted in the model, e.g. feces and respiration, a complete set of data is not absolutely necessary. However, the additional data do allow for alternative pathways in the model. For example, the regression equation for assimilation to respiration could have been used if the assimilation-to production equation was not satisfactory or needed improvement. If data for respiration had been missing, there would have been no alternative. By using different equations, it is possible to make predictions with incomplete data from the model. All parameters need better estimates, especially for Deep Creek, if precise predictions are the desired goal, but they are sufficient for the purpose of this study.

Energy budgets for *Enallagma anna, Ophiogomphus severus* and *Pyrrhosoma nymphula* are compared to the model's predicted budgets for *Argia vivida* and *P. nymphula* in Table I. All parameters for Deep Creek dragonflies are less than half of the corresponding values for *P. nymphula*, but in Deep Creek only one year is required for a complete life cycle. However, *Diplacodes trivialis*, which completes its life cycle in 4.5 months, has an energy budget very similar to the dragonflies in Deep Creek, especially *O. severus*, another anisopteran. Model predictions of assimilation efficiency are higher and the model values for feces are lower than the observed values for the respective parameters. For another dragonfly, *Lestes sponsa*, both WELCH (1968, from FISCHER, 1967) and FISCHER (1972) reported assimilation efficiencies of less than 50%. However, other carnivores studied by BROCKSEN, DAVIS & WARREN, (1968) assimilated 80-86% of what they consumed: the assimilation efficiency of two stoneflies, *Acroneuria pacifica* and *A. californica*, was 80.1-85.6% and that of two fish, *Salmo clarki* and *Cottus perplexus*, was 78.4-86.1%. The predicted and observed assimilation efficiencies agree closely with these values.

Since the model as constructed produces good general predictions, it could be used as a starting point for future models. By changing the constants if needed the model could be extended to other indvidual dragonflies and even entire populations. The present model might also be used as a subroutine in a computer simulation of an entire ecosystem.

Although the present model could be used in future models, much could be done to improve and refine it. By including photoperiod as a variable, new insights might be obtained into the seasonal regulation of growth and emergence. This additional variable would make the model more realistic. Manipulation of temperature and photoperiod could show which has the stronger influence on larval growth and emergence. The many studies which have been carried out on seasonal regulation would provide tests of predictions from the model. Reality and complexity could be increased further by introducing random effects and using new equations, e.g. differential equations. However, the increased compolexity could require more detailed and precise data to run and test the model. It was assumed in the model that production and consumption for *Pyrrhosoma nymphula* were reduced in the winter months, but the magnitude of the reduction was subjectively determined. Data in production and consumption are required to quantify these reductions in an actual population and so eliminate the subjective constraints. It may even be necessary to develop separate equations for the winter months. New equations may also be necessary to improve the predictions for small dragonflies (less than 3.5 mm). However, the key to the slow down of growth before winter could be more important in resolving that problem.

CONCLUSIONS

Tests of the model showed that it could be used to predict Lawton's data with a mean 10% error, except for feces, if production was reduced to zero the first winter and by half the second winter. Consumption was reduced to 0.0408 cal/mg dry wt/day during the winter months. Predictions for the complete life cycle of *Pyrrhosoma nymphula* were reasonable if the initial length was not below 3.5 mm and the starting date was in the first winter. This may indicate the need for different equations for small dragonflies. Additional test data were provided by laboratory growth experiments with *Argia vivida* and Enallagma *anna*. In predicting the growth of *A. vivida* in the laboratory with the model, all predictions were statistically different in slope from the observed, but some were visually close. Both Lawton's equations alone and in combination with Deep Creek equations were tested. In other tests there was good agreement of the predicted and observed growth of *A. vivida* in the field when fluctuating temperatures were used, but constant temperatures as found in one area of Deep Creek led to a predicted emergence in October. Finally, energy budgets, both predicted and observed, were compared for the dragonflies in this study. It was noted that *P. nymphula*, with a two year life cycle, uses over twice as much energy as the Deep Creek dragonflies which mature in one year, although both grow to a similar size.

Future revision and testing of the model should include photoperiod as a variable, random effect, and the use of differential equations to increase the realism and precision of the predictions from the model. Data on production and consumption when the temperature is less then 7°C are needed to verify the subjective assumptions that were made. Finally, the large differences between predicted and observed feces values could be reduced with additional information.

ACKNOWLEDGMENTS

I wish to thank Dr. G.W. MINSHALL for his help in preparing the manuscript and carrying out the research. Also, I would like to acknowledge MICHAEL SMOLEN for his advice in preparing the figures and CARYL TICKNER for her typing.

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